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The Male of *Megachile nivalis* Friese, with an Updated Key to Members of the Subgenus *Megachile* s. str. (Hymenoptera: Megachilidae) in North America

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Abstract.—The previously unknown male of *Megachile nivalis* Friese is described. Males of this species are very similar to those of *M. relativa* Cresson and because of geographic overlap of the two species, many male specimens presently identified as *M. relativa* within collections may actually be *M. nivalis*. An identification key and illustrations of mandibles are provided for females and males of the subgenus *Megachile* s. str. of North America. Images of genitalia, selected sterna, the lower genal area, clypeus, and forewings for males of both *M. relativa* and *M. nivalis* are also provided for comparison and to facilitate differentiation of the two species. A tabular summary is also provided for species of *Megachile* in North America that are known from only one sex to encourage the search for possible additional synonyms or hitherto unknown sexes.

Key words.—Apoidea, Megachilidae, *Megachile (Megachile)*, *Megachile nivalis*, male description, North America

Leafcutter and mason bees of the genus *Megachile* Latreille (Hymenoptera: Megachilidae) are a common and diverse group (Mitchell 1980, O'Toole and Raw 1991, Michener et al. 1994, Baker and Engel 2006) whose members display many morphological and behavioral adaptations (Michener 2000). Currently, 55 extant subgenera are recognized (Baker and Engel 2006), 30 of which are known from the western Hemisphere. In North America, thirteen subgenera are indigenous, but an additional three have been introduced (Michener 2000, Cane 2003). Hurd (in Krombein et al. 1979) listed 134 species of *Megachile* in North America north of Mexico (including the genus *Chalicodoma*); Michener et al. (1994) indicate 139 species. Since the publication of Krombein et al. (1979), at least 111 of the cataloged North American species have undergone changes in subgeneric allocation (Raw 2002), and Raw (2004) indicates that the 519 described species of *Megachile* in the Western Hemisphere are now allocated to their proper subgenus.

Much is known about the biology of many leafcutter bees due to their importance in crop pollination (Pengelly 1955, Osgood 1974, Ivanochko 1979, Peterson et al. 1992, Free 1993, Richards 1993, Delaplane and Mayer 2000, Raw 2002) and the fact that many species accept trap-nests (Medler 1959, 1964, Fye 1965, Krombein 1967, Frolich and Parker 1983, O'Toole and Raw 1991). Most members of the genus nest above ground in pre-existing cavities or excavate into pithy stems or decomposing wood (Stephen 1956, Ivanochko 1979). Trap-nesting of bees allows detailed study of life-history, nest building, provisioning and egg laying behaviors (Medler 1959, 1964, Klostermeyer and Gerber 1969, Frolich and Parker 1983, Kim 1992), and

incidences of cleptoparasitism (Scott et al. 2000); it also allows one to associate males and females of the same species. However, several North American species within the subgenera *Argyropile*, *Litomegachile*, *Megachiloides* (including *Derotropis* and *Xeromegachile*), and *Xanthosarus* (including *Delomegachile* and *Phaenosarus*) are ground-nesters (Eickwort et al. 1981, Williams et al. 1986, Krombein and Norden 1995), some exclusively so. Eickwort et al. (1981) indicate that nesting in pre-existing cavities is probably derived within the Megachilidae.

Difficulties in associating males and females in several groups of bees sometimes arise due to sexual dimorphism, and the comparatively ephemeral nature of males (Michener 2000). Unless specimens are collected and reared from nests (i.e., trap-nesting) or are caught during copulation, matching conspecifics of a given species is usually based on higher taxonomic classification, morphological similarities, geographic overlap, and speculation. Despite numerous studies, many North American bees are known from only one sex (Mitchell 1960), including 37% of described *Megachile* species (Table 1), and as a result the number of valid species for a given region may be significantly lower than suggested by catalogs (i.e., Krombein et al. 1979, Raw 2004). Because of their importance as pollinators, many bee collections are based on surveys from floral hosts which provide no knowledge of conspecifics, and other commonly used methods of mass collecting bees, such as Malaise traps and pan trapping, are equally problematic for similar reasons; although males do get collected, pairing them with their respective mates is not always possible. This issue is even more problematic for ground-nesting species (and their respective cleptoparasites); the nests of only a small proportion of these bees have been found or studied.

Molecular methods are commonly employed for analysis of bee phylogeny (Pedersen 1996, Danforth 1999, Danforth et al. 2006 a and b), revealing cryptic species (Carman and Packer 1996, Packer and Taylor 1997, Hebert et al. 2004, Simmons and Scheffer 2004) and more recently have been advocated for accurate identification of organisms to species level (Hebert et al. 2003, Savolainen et al. 2005), including insects (Pinto et al. 2003). As such, molecular methods offer much hope for associating male and female conspecifics of sexually dimorphic organisms (Pilgrim and Pitts 2006).

Megachile Subgenus *Megachile* Latreille s. str

The subgenus *Megachile* s. str. is a holarctic group found mostly in cool climates (Michener 2000), and five species are currently recognized in the western hemisphere (Mitchell 1935, 1962). *Megachile* s. str. are common members of temperate, boreal and subarctic North America, ranging from Nova Scotia (Sheffield et al. 2003) and Newfoundland through to Alaska and as far south as Mexico (Mitchell 1962). The North American species are *M. centuncularis* Linnaeus, *M. inermis* Provancher, *M. montivaga* Cresson, *M. nivalis* Friese and *M. relativa* Cresson; *M. centuncularis* has a holarctic distribution (Mitchell 1935, Michener, 2000) and is occasionally bivoltine in parts of its North American range (C.S. Sheffield, personal observations in Nova Scotia, Canada). Three species, *M. centuncularis*, *M. inermis* and *M. relativa* are collected commonly in trap-nest surveys within Canada and the northern United States (Stephen 1956, Medler 1959, Fye 1965, Krunic and Salt 1971, Ivanochko 1979, Sheffield 2006). In recent trap-nest surveys in Nova Scotia (Sheffield 2006), these three species accounted for 3.6%, 13.8% and 21.4% of all bees collected, respectively, surpassed only by *Osmia tersula* Cockerell (Osmiinae). *Megachile inermis* also has been recorded nesting in decaying wood (Mitchell 1935, Stephen 1956). *Megachile montivaga* differs from

Table 1. North American species of *Megachile* (Hymenoptera: Megachilidae) known from only one sex, and suggested conspecific or synonomy.

Subgenus	Species, author	Described sex: Female	Described sex: Male	Suggested conspecific or synonym
Argyropile	*asterae* Mitchell	♀		
	rossi Mitchell	♀		
	sabinensis Mitchell	♀		
	tulariana Mitchell	♀		
Chelostomoides	*cartagenensis* Mitchell		♂	
	subspinotulata Mitchell	♀		
Megachile	*nivalis* Friese	♀		
Megachiloides	*alamosana* Mitchell		♂	
	anograe Cockerell	♀		
	boharti Mitchell	♀		
	bradleyi Mitchell	♀		
	bruneri Mitchell		♂	♂ of *M. hilata* Mitchell
	coloradensis Mitchell	♀		
	dulciana Mitchell	♀		
	hilata Mitchell	♀		♀ of *M. bruneri* Mitchell
	hookeri Cockerell	♀		Possible syn. of *M. nevadensis* Cresson
	impartita Mitchell	♀		
	instita Mitchell		♂	
	inyoensis Mitchell	♀		
	laguniana Mitchell	♀		
	latita Mitchell	♀		
	laurita Mitchell	♀		
	macneilli Mitchell		♂	
	maurata Mitchell		♂	
	melanderi Mitchell	♀		
	micheneri Mitchell		♂	
	mojavensis Mitchell	♀		
	nelsoni Mitchell	♀		
	oslari Mitchell	♀		
	pagosiana Mitchell	♀		
	parksi Mitchell	♀		
	pseudolegalis Mitchell		♂	
	pseudonigra Mitchell	♀		
	seducta Mitchell	♀		
	semilaurita Mitchell	♀		
	stoddardensis Mitchell		♂	
	subanograe Mitchell	♀		
	sublaurita Mitchell	♀		
	toscata Mitchell	♀		
	victoriana Mitchell		♂	
	wyomingensis Mitchell		♂	
	yumensis Mitchell	♀		
Neochelynia	*aegra* Mitchell		♂	♂ of *M. chichimeca* Cresson
	chichimeca Cresson	♀		♀ of *M. aegra* Mitchell
Pseudocentron	*morio* Smith	♀		Possible form of *M. pruina* Smith
	pruina nigropinguis Mitchell	♀		
Sayapis	*dentipes* Vachal		♂	
	helianthi Cockerell	♀		
	pugnata pomonae Cockerell	♀		
Xanthosarus	*gemula cressonii* Dalla Torre	♀		
	giliae Cockerell		♂	♀ known, but not described

other members of the subgenus in that it lacks the mandibular cutting edges (Fig. 1) and uses flower petals for nest cell construction (Mitchell 1935, Michener 2000). Unlike the preceding three species, *M. montivaga* does not appear to accept trap-nests and instead nests in pithy plant stems as well as in soil (Ivanochko 1979). Mitchell (1935) indicates variability in nesting site choice/substrate for these four species.

In contrast to the preceding species which range as far south as Texas and Mexico, *M. nivalis* appears to have a more northern distribution (Mitchell 1935, 1962, Ivanochko 1979, Krombein et al. 1979). Little is known about its nesting biology but apparently females have been excavated from a river bank in the Yukon Territory in Canada along with other *Megachile* species: *M. giliae* Cockerell (♂'s only), *M. montivaga*, *M. relativa*, and *M. frigida* Smith (Ivanochko 1979). Males of *M. nivalis* have never been described (Mitchell 1935, 1962, Ivanochko 1979). Mitchell (1935, 1942, 1962) and Ivanochko (1979) indicate the similarity of female *M. nivalis* to *M. relativa* (and to a lesser extent, *M. centuncularis*), the main distinguishing characters being differences in the color and length of the pubescence on T6, and the color of the scopal hairs on S6 (Mitchell 1935, 1962, Ivanochko 1979); *M. nivalis* females are also generally larger than those of *M. relativa* (Mitchell 1942). Mitchell (1942) suggested that *M. nivalis* may represent a race of *M. relativa*, and speculated that the male would be very similar to that of *M. relativa* (Mitchell 1935). He subsequently (Mitchell 1942, 1962) examined specimens of male *Megachile* (not collected *in copula*) and suggested they may be related to female *M. nivalis*. However, he could not distinguish these males from those of *M. relativa* (Mitchell 1962).

Megachile giliae, with no described female (but with a northern distribution that overlaps with that of *M. nivalis*) has been indicated as the possible conspecific of *M. nivalis* (Mitchell 1935, Ivanochko 1979), but this association seems unlikely since morphologically, it classifies within the subgenus *Xanthosarus* (Mitchell 1935, Krombein et al. 1979 as subgenus *Delomegachile*). However, the female of *M. giliae* has been collected and identified (see McGuire 1993, Bishop and Armbruster 1999), although no published descriptions presently exist.

In 2005, a trap-nest survey conducted in Yellowknife, Northwest Territories yielded many female *M. nivalis*, ten specimens of a male *Megachile*, and a male and female of the cleptoparasite, *Coelioxys funeraria* Smith (Megachilidae). Examination of genitalia (Figs 2, 3) and S5, S6 and S8 (Fig. 4) of *M. relativa* and the newly collected male specimens revealed similarities, but consistent and distinct differences were noted (see below). Additional differences between the Yellowknife males and *M. relativa* were observed on the lower genal area (Fig. 5), the clypeal margin (Fig. 6), and in wing venation (Fig. 7) – further details are provided below. These new specimens confirm the association of male *M. nivalis* with the female, and an updated key to the North American members of the subgenus *Megachile* s. str. is provided. The specimens are currently held in the senior author's collection, but material will also be placed in the Packer Bee collection, York University, Toronto, ON and the Canadian National Collection, Ottawa, ON upon completion of this study.

Diagnosis of Megachile s. str.—The body length of the subgenus varies considerably, from 7–20 mm (Michener 2000); *M. inermis* being the largest North American species. Females of *Megachile* s. str. can be separated from other North American subgenera by the five-dentate mandibles, with the fourth tooth separated from the inner tooth by a broad and shallow interspace which lacks a cutting edge (Fig. 1), including *M. montivaga*, although the indentation between the two inner teeth is obscure (Fig. 1a). *Megachile* s. str females also have a single incomplete cutting edge in the second interspace (Fig. 1) which is some-

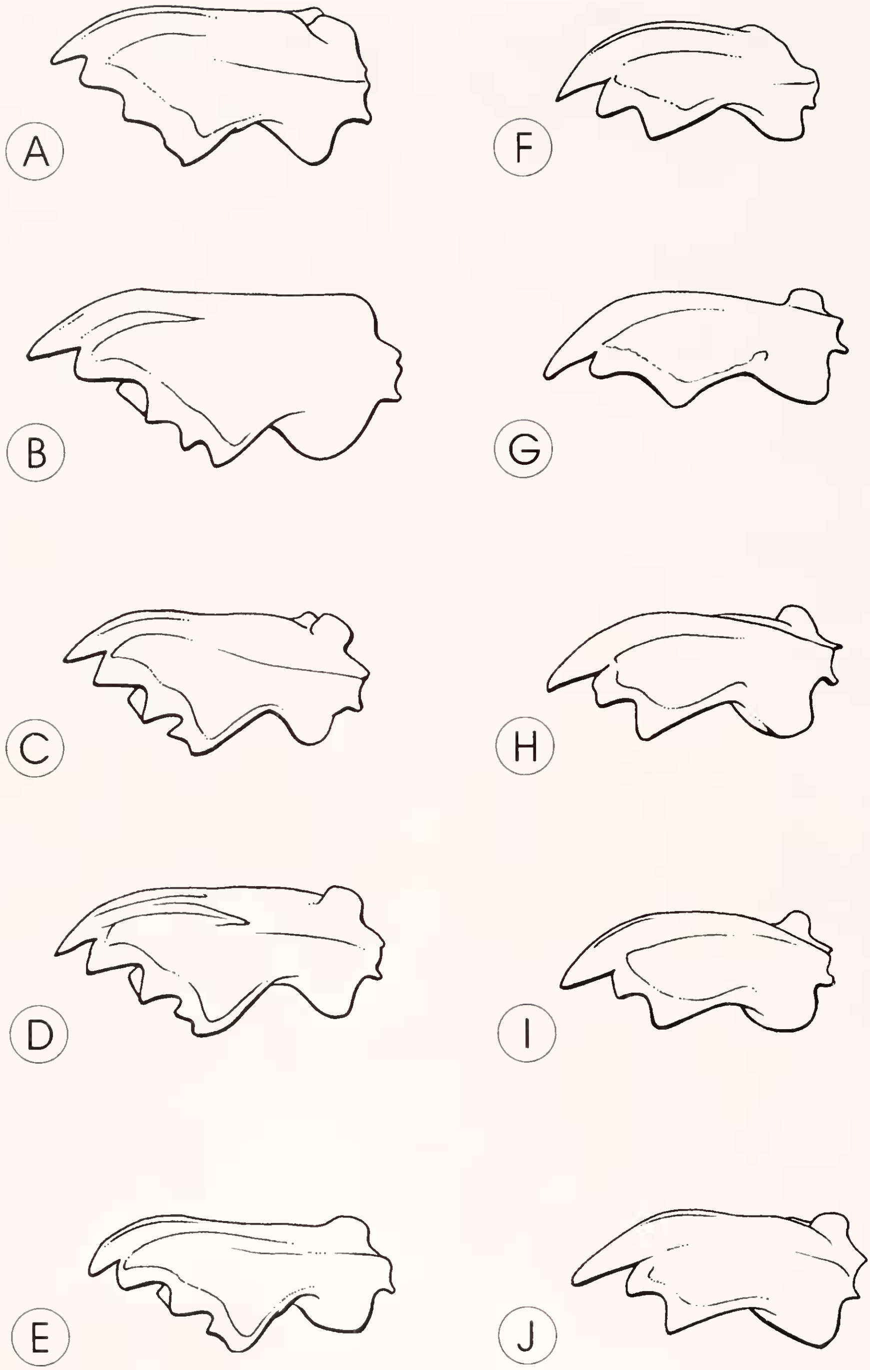

Fig. 1. Mandibles of female (left column) and male (right column) *Megachile* s. str.: *M. montivaga* (A and F); *M. inermis* (B and G); *M. centuncularis* (C and H); *M. relativa* (D and I); *M. nivalis* (E and J).

Fig. 2. Dorsal and lateral views of genital capsules of *Megachile relativa* (A and C) and *M. nivalis* (B and D).

what reduced in *M. relativa* (Michener 2000) and absent in *M. montivaga* (Fig. 1a). Female *M. montivaga* also differs from the other four species as T6 is concave in profile, not straight. The scopal hairs are uniformly colored, ranging from fulvous to ochraceous; in *M. nivalis* the scopal hairs of S6 (and often S5) are black, not concolorous

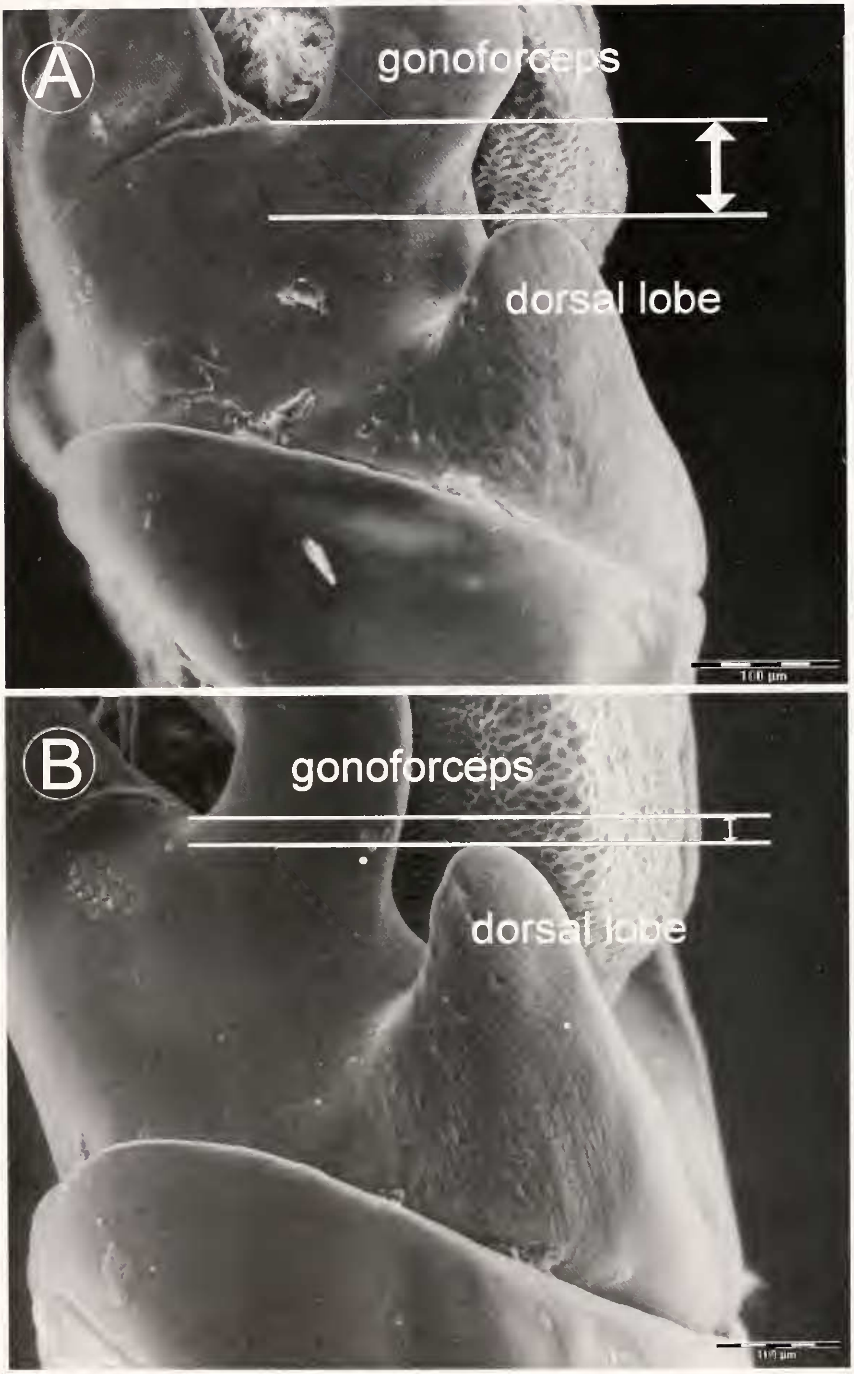

Fig. 3. Close up of lateral views of genitalia for *Megachile relativa* (A) and *M. nivalis* (B). Horizontal lines and double-ended arrows show relative length of dorsal lobe of gonocoxite to base of gonoforceps. Scale bars represent 100 µm.

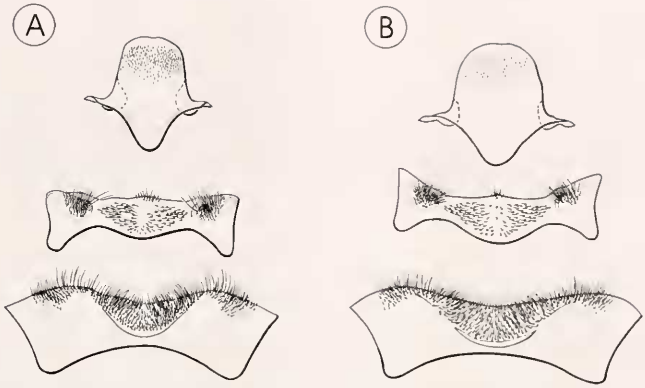

Fig. 4. Sterna V (bottom), VI (middle) and VIII (top) of male *Megachile relativa* (A) and *M. nivalis* (B).

with those of the preceding sterna which are ochraceous.

Males have three-dentate mandibles, and the teeth are equally spaced except in *M. inermis* (Fig. 1g). The mandibles also possess a narrow, distinct, basal or subbasal, inferior process (Fig. 5a), the shape of the apical margin of this process varies slightly among species. The front coxa of male *Megachile* s. str. are hairy, with no spine and no patch of rufescent bristles, the exception being males of *M. montivaga* in which the front coxal spines are present, represented by dentiform tubercles which are often difficult to see. Further descriptions of this subgenus can be found in Mitchell (1935), Ivanochko (1979), and Michener (2000). Descriptions of the North American species are found in Mitchell (1935, 1962) and Ivanochko (1979).

The subgeneric assignment of *M. montivaga* has come into question (Mitchell 1980, Michener 2000) due to the exceptions listed above. In addition, this species collects rose

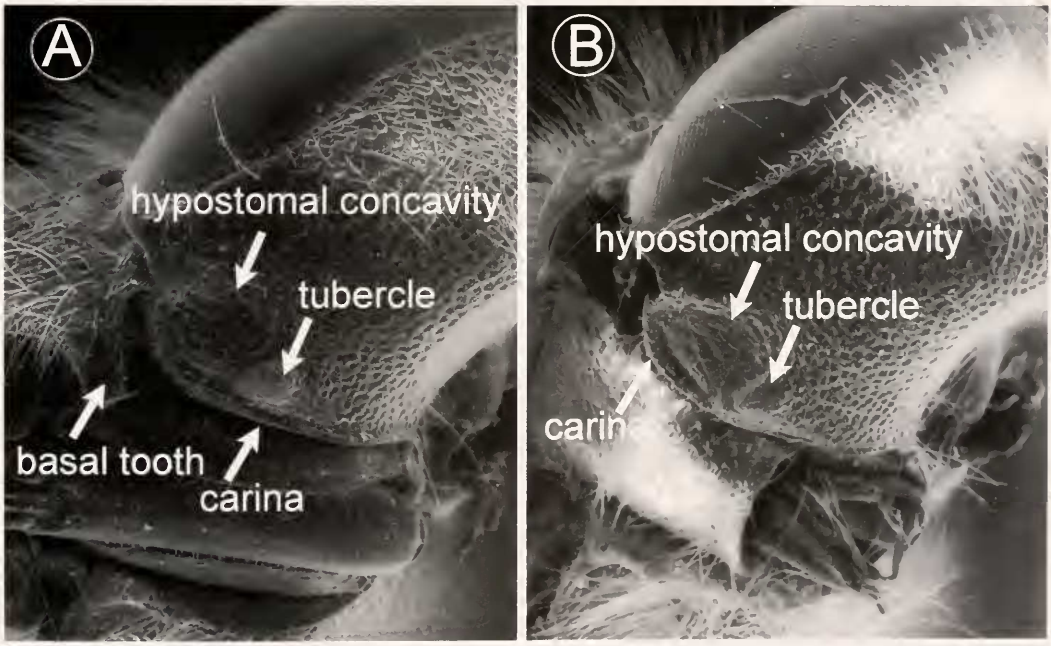

Fig. 5. The lower genal area of male *Megachile relativa* (A) and *M. nivalis* (B).

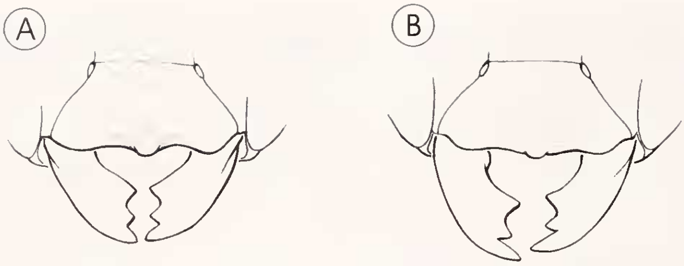

Fig. 6. Clypeal margins of male *Megachile relativa* (A) and *M. nivalis* (B).

petals instead of leaves for nest construction (Mitchell 1935, Michener 2000), and unlike the remaining four species, *M. montivaga* does not appear to accept trap-nests. Robertson (1903) proposed the generic name *Cyphopyga* just for *M. montivaga*. However, Mitchell (1935) indicated that the morphological differences were at the species level and had no real generic or even subgeneric value, especially when the genitalia and hidden sterna of the males were considered. Despite this, he later (Mitchell 1980) recognized *Cyphopyga* as a four-toothed subgenus of *Megachile*, with *M. montivaga* as the only species, but Michener (2000) considered it unnecessary to recognize a unique supraspecific taxon for this species alone.

KEY TO NORTH AMERICAN BEES OF THE SUBGENUS *MEGACHILE* LATREILLE S. STR.

The key provided is based on those provided elsewhere (Mitchell 1962, Ivanochko 1979) and through examination of specimens collected throughout Canada and currently held in the senior author's collection, and the Packer Bee collection, both at York University. The description of male *Megachile nivalis* is based on examination and dissection of the ten specimens collected in Yellowknife, NT in 2005. In mention of genitalia, gonoforceps refers to the distal (free) part of the gonocoxite plus the apical gonostylus.

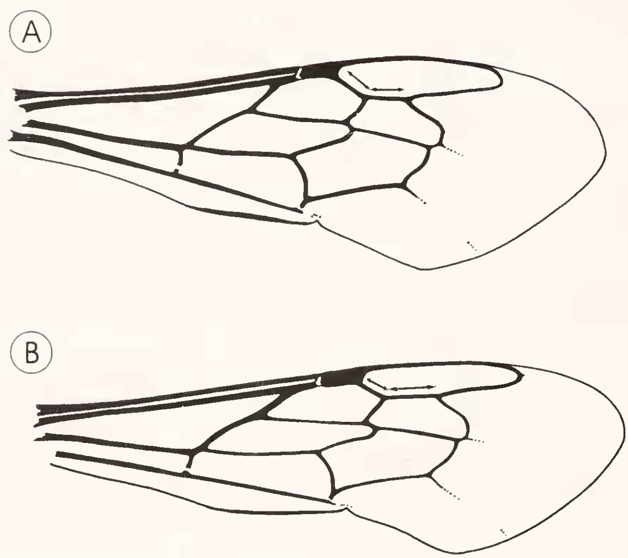

Fig. 7. Forewings of male *Megachile relativa* (A) and *M. nivalis* (B). Double ended arrows show the relative lengths of vein r (first submarginal cell) to Rs (second submarginal cell), r being much shorter in *M. nivalis*.

FEMALES

1 a. Scopal hairs on S6 (and often S5) black .... *nivalis* Friese
b. Scopal hairs entirely pale fulvous or ochraceous 2
2 a. T6 with a mixture of very short, suberect or appressed pubescence and abundant, long and erect pubescence which is visible in profile 3
b. T6 with few erect hairs, showing mostly very short, sub-erect or appressed pubescence in profile 4
3 a. Pubescence of T6 entirely dark .... *centuncularis* Linnaeus
b. T6 with erect and appressed golden tomentum .... *relativa* Cresson
4 a. T6 concave in profile; mandibles entirely lacking a cutting edge (Fig. 1a); punctures of clypeus and supraclypeal area coarse and close, interspaces much less than their diameter up to the edges of the distinct median impunctate line; interocellar distance subequal to distance of ocelli from edge of vertex; smaller species (<11 mm) .... *montivaga* Cresson
b. T6 straight in profile; mandibles with a distinct cutting edge in the second interspace (Figs 1b–e), surface of clypeus and supraclypeal area highly polished in central third, especially on apical ends, surface impunctate and/or with interspaces much greater than puncture diameter; interocellar distance much less than the distance from ocelli to edge of vertex; larger species (13 mm or more) .... *inermis* Provancher

MALES

For users of Mitchell's (1962) "Bees of the Eastern United States", substitute couplets 2 and 3 below into his couplet 17 – page 113)

1. a. Distance from the apex of the middle tooth to the apex of the inner tooth nearly twice as great as the distance from the apex of the middle tooth to the apex of the outer tooth (Fig. 1g); interocellar distance much less than the distance from ocelli to edge of vertex; larger species (13 mm or more) .... *inermis* Provancher
b. Distance from the apex of the middle tooth to the apices of either the inner or outer teeth subequal (Figs 1f, h–j); interocellar distance subequal to distant from ocelli to edge of vertex; smaller species (<12 mm) 2
2. a. Clypeal margin with a distinct median tubercle (Fig. 6); surface of T6 polished above carina, the central punctures separated by their diameter 3
b. Clypeal margin not tuberculate, but possibly narrowly produced medially (a few minute crenulations may also be visible medially in *M. montivaga*); surface of T6 either more closely punctate (the interspaces less than one puncture diameter) or surface tuberculate 4
3. a. Hypostomal tubercle short (Fig. 5a); hypostomal concavity shallow and not well defined (Fig. 5a); hypostomal carina distinct for most of its length (pile must be removed to see these features) (Fig. 5a); clypeal margin sinuous on either side of the prominent, shining, median tubercle (Fig. 6a); dorsal lobe of gonocoxite short, not attaining the base of gonoforceps (Fig. 3a), its length subequal to the width of gonobase (Figs 2a and c); vein r of the first submarginal cell normally subequal to vein Rs of the second submarginal cell (Fig. 7a) .... *relativa* Cresson
b. Hypostomal tubercle more prominent and wider at base (Fig. 5b); hypostomal concavity deeper and well defined; hypostomal carina interrupted by the hypostomal tubercle (Fig. 5b); clypeal margin slightly curved to nearly straight on either side of the less prominent, median tubercle (Fig. 6b); dorsal lobe of gonocoxite long, fully attaining the base of gonoforceps (Fig. 3b) and longer than the width of gonobase (Figs 2b and d); vein r of the first submarginal cell shorter than vein Rs of the second submarginal cell (Fig. 7b) .... *nivalis* Friese

4. a. Coxal spines represented by dentiform tubercles; carina of T6 with a definite median emargination, apical margin of the segment with conspicuous inner teeth and spine-like lateral teeth, the surface above the carina dull, minutely rugosopunctate . . . . *montivaga* **Cresson**

b. Coxal spines entirely lacking; carina of T6 with an obscure median emargination, the apical margin of the segment with broad inner teeth and obscure lateral teeth, the surface above the carina with numerous small tubercles, the punctures very obscure . . . . *centuncularis* **Linnaeus**

Megachile nivalis Friese

Megachile nivalis Friese, 1903. Ztschr. System. Hym. Dipt. 3: 246. ♀

Megachile (Anthemois) santiamensis Mitchell, 1934. Trans. Am. Ent. Soc. 59: 311. ♀

Megachile (Anthemois) nivalis Mitchell, 1935. Trans. Am. Ent. Soc. 61: 174. ♀

Megachile (Anthemois) nivalis Mitchell, 1942. Pan-Pacific Ent. 38: 15–16. ♀ (♂ misdet.)

Megachile (Megachile) nivalis Mitchell, 1962. North Carolina Ag. Exp. Stat. Tech. Bull. 152: 129. ♀

Description of male presented here follows format used by Mitchell (1962).

Male.—Length 9–12 mm; entirely black except as follows: tegula testaceous along margins, basal tarsal segment black to somewhat reddened, following segments reddish testaceous; eyes slightly convergent below; clypeal margin nearly straight on either side of a distinct but small median tubercle (Fig. 6b); mandible three-dentate, with a rather narrow, sub-basal, inferior tooth which is subtruncate apically (Fig. 5a – *Megachile relativa*, but similar in structure); apical segment of flagellum slender and elongate; distance of lateral ocellus from margin of vertex and from margin of eye subequal; cheek somewhat broader than compound eye; punctures fine, slightly separated across vertex posteriorly, sparse between ocelli and eye, becoming close on cheek above and densely crowded or rugose below; face below ocelli rather coarsely rugosopunctate, becoming finely so below antennae and on clypeus; hypostomal depression well defined (Fig. 5b), hypostomal tubercle long and relatively prominent, broadly interrupting hypostomal carina (Fig. 5b); pubescence golden, becoming paler on lower part of cheek, quite long and copious around antenna and lower part of face, on cheek below and on thorax laterally and posteriorly; vertex with an admixture of pale and black pubescence; mesoscutum and scutellum with more or less intermixed light and dark hairs which are quite long and erect but thin; mesoscutum dull, punctures close, shallow, not very coarse, slightly separated only in center of disc; punctures of scutellum slightly separated along mid-line, but otherwise quite uniformly close, those on axilla much finer and densely crowded; pleura dull, punctures shallow, quite close and poorly-defined; propodeum relatively smooth and shining; basitarsi quite short and slender; mid tibial spur short but well developed; tegula shining, rather uniformly, minutely and rather closely punctate; wings subhyaline, veins brownish, vein r of the first submarginal cell shorter than vein Rs of the second submarginal cell (Fig. 7b); T2–T4 shallowly grooved or depressed across base, basal margin of grooves not distinctly carinate, apical margins of terga depressed only toward sides, depressed medially only on T4 and T5, pale apical fasciae evident at extreme sides of the more basal terga, more or less complete on T4 and T5, discal pubescence rather thin, largely black but with pale hairs evident toward sides, length of discal pubescence exceeding apical margin of all terga when viewed laterally, basal tergum covered with copious, elongate, whitish pubescence; punctures very fine, surface

shining, close on T2 barely evident on T1, quite sparse on T3 and T4, becoming somewhat coarser laterally, but still well separated, T5 with somewhat closer and coarser punctures throughout; T6 shining, carina very low, broadly and shallowly incurved medially, punctures fine and close above carina, separated by their diameter, becoming somewhat more coarse and sparse laterally, inner teeth of apical margin broadly carinate, widely separated, relatively near the short, acute, lateral teeth; T7 quite prominent, broad and short, with a deep excavation on dorsal surface; S1–S4 exposed, closely but rather obscurely punctate, apical margins of S2–S4 broadly yellowish-hyaline and with thin, apical fringes of pale hairs; setose area of S5 restricted, finely setose (Fig. 4); S6 sparsely setose on each side, apical lobe barely evident (Fig. 4); gonoforceps slender with acute apex, gonocoxite basally with a distinct dorsal lobe which fully attains the base of gonoforceps (Figs 2 and 3).

Distribution.—The type locality for *Megachile nivalis* is Pikes Peak, Colorado (Mitchell 1935). This species is most common in northwestern areas of North America, having been reported from Alaska, Yukon Territory, Northwest Territories, British Columbia, Alberta, Saskatchewan, Manitoba, Ontario and Quebec. It is less common in the southern limits of its range which include Washington, Oregon, Idaho, Montana, Wyoming, Minnesota, and Colorado. It has also been reported from Maine (Mitchell 1962).

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